NEOTROPICAL BIOLOGY AND CONSERVATION

Neotropical Biology and Conservation 20(3): 221–246 (2025)
DOI: 10.3897/neotropical.20.e154485

Research Article

# Cohabitation networks: exploring how termites and ants share nests in Amazonian forests

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## Abstract

Cohabitation between ants and termites is a widespread yet understudied ecological interaction in tropical forests. This study explores the patterns of termite–ant cohabitation networks across different forest coverages in the Colombian Amazon, focusing on taxonomic composition, nesting substrates, and ant functional guilds. A total of 413 specimens were collected from 283 cohabitation networks, identifying 197 interacting species (110 ants and 87 termites). The network exhibited moderate connectance (C = 0.279) and high modularity (Q = 0.602), indicating that only a subset of potential interactions occurred, with distinct species groups forming stronger intragroup connections. Ant genera such as *Pheidole*, *Camponotus*, *Crematogaster*, *Acropyga*, and the species *Pseudoponera stigma* played central roles, interacting with multiple termite genera, while termite genera like *Nasutitermes*, *Heterotermes*, and *Araujotermes* emerged as key nodes due to their nesting habits and high abundance. Cohabitation patterns varied across forest types, with primary forests supporting more complex networks than secondary forests, underscoring the importance of habitat conservation in maintaining biodiversity. Wood-based nests supported the highest diversity of cohabiting ants, and generalist ants—particularly *Pseudoponera stigma* and species of *Pheidole*—were frequent connectors across modules. These findings provide new insights into the ecological mechanisms underlying termite–ant cohabitation and emphasize the importance of preserving structurally complex habitats to maintain these interactions.

**Key words:** Bi-partite network, Formicidae, guild, Isoptera, nesting substrate

OPEN ACCESS

Academic editor: Patricia Nunes-Silva
Received: 1 April 2025
Accepted: 14 July 2025
Published: 28 August 2025

ZooBank: https://zoobank.org/9B476638-906C-4D65-A8DB-AFC247AAA151

Citation: Castro D, Fernández F (2025) Cohabitation networks: exploring how termites and ants share nests in Amazonian forests. Neotropical Biology and Conservation 20(3): 221–246. https://doi.org/10.3897/neotropical.20.e154485

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## Introduction

In tropical ecosystems, interspecific interactions are fundamental in shaping community structure and ecosystem functioning (Tylianakis et al. 2008). Among these interactions, cohabitation—the shared use of nesting sites by multiple species—represents an ecological strategy. In termites, cohabitation often involves not only ants but also inquiline termite species, fungi (e.g., *Termitomyces*), and microbial partners, forming complex macrosymbiotic systems that contribute to nutrient cycling and nest stability (Aanen and Boomsma 2005; Aanen et al. 2007; Florencio et al. 2013). Nest-sharing between termites and ants can be driven by a combination of ecological factors, including

competition for nesting sites, mutualistic benefits, and habitat filtering (Dejean and Bolton 1995; Diehl et al. 2005; Marins et al. 2016). Termites and ants, two dominant groups of soil and arboreal invertebrates (Tuma et al. 2020), frequently engage in cohabitation, forming intricate networks of associations that range from facultative cohabitation to obligatory symbioses (Hölldobler and Wilson 2009; Jouquet et al. 2011). Network-based analyses suggest that even cryptic termite–termite cohabitation patterns, which are not directly observable, may be predominantly mutualistic, highlighting the value of emergent network properties to infer interaction types in concealed systems (Campbell et al. 2016).

Termite–ant cohabitation dynamics are shaped by a combination of nest characteristics, species interactions, and environmental factors. Termites often construct large, long-lived nests that provide stable microclimatic conditions, which may be exploited by secondary occupants such as ants (Korb 2010; Cristaldo et al. 2012), since termite inquilinism within ant nests is less common (Crist and Friese 1994; Diehl et al. 2005). In some cases, cohabiting ants may contribute to termite nest defense or nutrient cycling. For instance, in Neotropical systems, certain ant species have been observed preying on dead termites while providing protection against predators and contributing nitrogen-rich nutrients to termite colonies, suggesting an incipient form of facultative mutualism (Jaffe et al. 1995). Similarly, in non-Neotropical systems, some termitophilous ants appear to defend termite mounds from aggressive intruders, benefiting termite colony survival (Higashi and Ito 1989). Understanding the ecological drivers of termite–ant cohabitation requires a comprehensive approach that considers environmental heterogeneity and species-specific traits (Viana-Junior et al. 2021).

The likelihood and diversity of these interactions depend on abiotic and biotic conditions. Nest volume (Cristaldo et al. 2012), elevation (Viana-Junior et al. 2021), fire (Marins et al. 2016), and the presence of the builder species (Crist and Friese 1994) all influence the structure of invertebrate communities within termite nests. However, despite their ecological significance, the drivers of termite–ant cohabitation remain poorly understood, particularly in hyperdiverse regions like the Neotropics (Antonelli et al. 2018). Most studies have focused on species that construct large and abundant nests, as these structures are more easily detectable and provide stable habitats for secondary occupants (Jaffe et al. 1995; Diehl et al. 2005; Prestes and Cunha 2012; Gallego-Ropero et al. 2013; Marins et al. 2016), or have been limited to leaf litter substrates (Mertl et al. 2012). However, generalist cohabitation—where species with discrete and cryptic nesting habits share nests—has been largely overlooked. This gap in knowledge challenges our understanding of interaction networks and the ecological processes shaping nest-sharing dynamics in tropical ecosystems. From a broader perspective, this study helps address what Hortal et al. (2015) define as the Eltonian shortfall: the lack of information on species interactions and their functional roles within ecosystems. While gaps in taxonomic and distributional knowledge (Linnean and Wallacean shortfalls) have historically dominated biodiversity research (Bini et al. 2006), understanding biotic interactions remains a critical and often neglected frontier.

Forest cover and conservation status are known to influence biodiversity and ecological interactions in tropical forests by altering microhabitats, resource availability, and structural complexity (Atangana et al. 2014; Solar et al. 2016;

Pillay et al. 2022). For termite–ant cohabitation, we hypothesize that primary forests, due to their greater structural complexity and higher diversity of nesting substrates, will support more complex and diverse interaction networks than secondary forests (Bandeira 1979; Floren and Linsenmair 2005; Luke et al. 2014).

Additionally, seasonally flooded forests differ markedly from terra-firme forests in terms of hydrological dynamics, which can limit the establishment and persistence of termite nests due to periodic inundation (Martius 1997). This environmental constraint likely reduces the diversity and availability of nesting substrates (Martius 1994, 2001), thereby influencing the opportunities for ant–termite cohabitation. In such conditions, termite nests may serve as critical refuges from flooding and environmental instability, potentially increasing their occupation by ants seeking stable nesting sites. We therefore expected higher frequencies of cohabitation in seasonally flooded forests, where stress-induced nesting limitations may drive secondary occupation—a pattern previously observed under other forms of environmental stress, such as fire and elevation (Monteiro et al. 2017; Viana-Junior et al. 2021).

In complex ecological systems, species interactions are often structured into distinct subgroups or modules, where subsets of species interact more frequently among themselves than with others (Newman 2006; Bascompte 2010). These modular structures can reflect ecological affinities, microhabitat preferences, or niche complementarity and are considered emergent properties of ecological networks (Olesen et al. 2007; Dáttilo et al. 2016). The identification of species that act as structural connectors or hubs within these networks has proven useful to understand how individual taxa influence the cohesion and organization of interaction networks (Guimerà and Amaral 2005; Mello et al. 2019). In poorly known systems such as termite–ant cohabitation networks, where interactions are often cryptic and structurally complex, this topological perspective offers a complementary view on the functional roles that species may play, especially in relation to habitat specialization, dominance, or ecological generalism (Tuma et al. 2020). Modularity and topological roles thus provide a conceptual framework to explore how cohabiting ants and termites organize their associations across forest types and environmental gradients.

Building on this foundation, we investigate the patterns of termite–ant cohabitation networks in Amazonian forests from a high-level taxonomic perspective, assessing how nest-sharing patterns vary across different forest coverages. By integrating field observations and ecological analysis, this study contributes to a better understanding of species interactions and their role in structuring invertebrate communities in tropical ecosystems. This study aims to characterize the taxonomic composition of termite–ant interaction networks, exploring how these interactions vary across different nesting substrates and ant functional guilds. Additionally, we compare these networks across distinct Amazonian forest coverages to assess the influence of forest cover on cohabitation patterns. Given the environmental contrasts among forest types, this comparison provides insights into how habitat heterogeneity and anthropogenic pressures influence cohabitation networks. By integrating taxonomic, ecological, and network-based approaches, we seek to provide a comprehensive understanding of the mechanisms driving termite–ant cohabitation in one of the world's most biodiverse biomes.

# Methods

## Study area

This study was conducted in four departments of the Colombian Amazon: Amazonas, Vaupés, Guainía, and Guaviare. A total of 30 sites were sampled, including 20 sites in Amazonas, two in Vaupés, four in Guainía, and four in Guaviare (Fig. 1). Sampling was carried out on different dates between January and November from 2002 to 2004. Elevation ranged from 97 to 279 m above sea level, with geographical limits between latitudes −4.0468 and 3.8166 and longitudes −73.2699 and −67.5243 (Suppl. material 1).

Four forest coverages were sampled, based on two main forest types: terra-firme forests, which are upland forests that do not experience seasonal flooding and grow on well-drained soils, and seasonally flooded forests (locally known as *várzeas* or *rebalses*), which are lowland forests subject to periodic inundation due to topography and high rainfall during the wet season (Pires and Prance 1985; Bredin et al. 2020).

Within each forest type, we considered conservation status by classifying sites as either primary forests, which have never been subjected to anthropogenic disturbance, or secondary forests, which have experienced human intervention but have been undergoing natural succession for at least 20 years. In the departments of Amazonas and Guainía, anthropogenic disturbances in secondary forests are primarily associated with selective logging for local construction and the establishment of traditional indigenous agroecosystems known as *chagras* or *conucos*. In contrast, secondary forests in Guaviare are

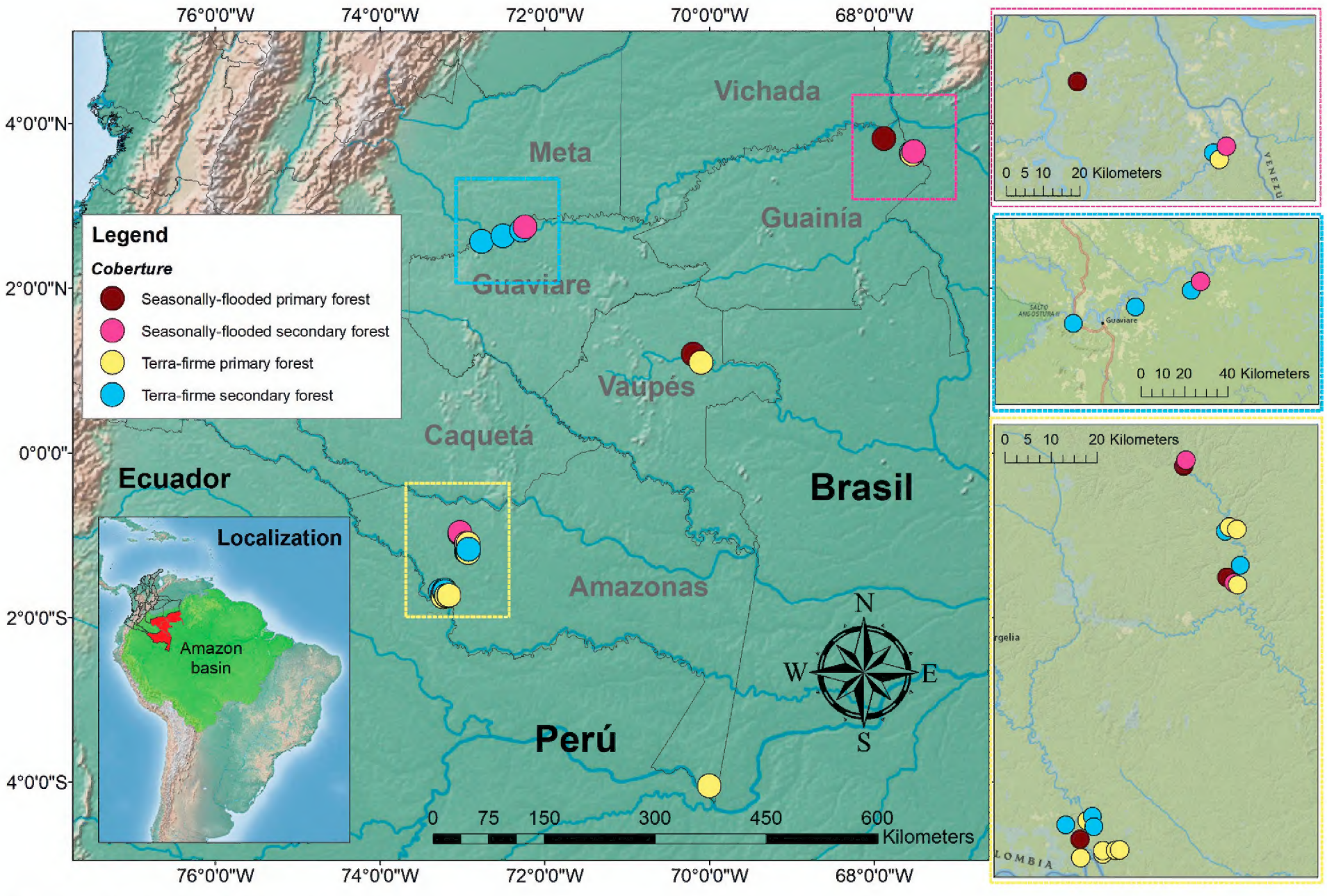


**Figure 1.** Location of the sampling sites.

subject to more intense pressures from agricultural expansion and cattle ranching, reflecting broader trends in deforestation linked to frontier dynamics. The number of sites per coverage was as follows: five sites in seasonally flooded primary forest, four in seasonally flooded secondary forest, 12 in terra-firme primary forest, and nine in terra-firme secondary forest.

## Field sampling

The specimens analyzed in this study were collected using a modified version of the transect protocol (Jones and Eggleton 2000; Dambros et al. 2020) adapted for termite diversity research. The standardized protocol across all sites involved a 250 m transect divided into eight plots, each measuring 5 m × 2 m, with a 30 m spacing between plots.

In each plot, two collectors actively searched for termites in different nesting substrates (nests and single-piece nests, Constantino 2020) for 25 minutes. When termites and ants were found co-occurring within the same physical structure, they were recorded as cohabiting. We applied a strict spatial criterion for the cohabitation occurrences: ants were considered cohabitants only when observed inside galleries, chambers, or tunnels actively occupied by termites, with multiple individuals of termites or both groups in some cases sharing the same microstructure (e.g., a gallery system or feeding chamber). This approach excluded the incidental presence of ants in the general vicinity or on the surface of the substrate. Approximately 10 individuals per caste were collected for termites, while for ants, up to 10 individuals were sampled whenever possible. All specimens were captured using aspirators and preserved in plastic vials containing 96% ethanol. To preserve the physical evidence of cohabitation, individuals from both groups were stored together in the same vial until laboratory processing.

Additionally, the type of nesting substrate was recorded, with nests classified according to their structure (Noirot and Darlington 2000) and feeding substrates categorized as follows: soil, epigeal nest, aerial nest, wood (dry, minimally decomposed pieces), and wood/soil (highly decomposed wood, characterized by the lack of xylophagous material).

## Termite and ant taxonomic identification, and feeding guilds of ants

For termite identification, morphological characters of the soldier caste were used to determine species. Keys, generic revisions, and original descriptions were used to identify termite species (Emerson 1925, 1952; Krishna and Araujo 1968; Mathews 1977; Constantino 1990, 1995, 2002; Cancello and Noirot 2003; Krishna 2003; Constantino et al. 2006; Rocha and Cancello 2007, 2022; Carrijo et al. 2011, 2020, 2023; Cuezzo and Nickle 2011; Rocha et al. 2012; Hellemans et al. 2017; Castro and Scheffrahn 2019). An exception was made for the Apicotermitinae subfamily, where identification was based on the dissection of the worker enteric valve (Castro et al. 2020); for these soldierless termites, undescribed species were morphotyped, and their enteric valves were photographed and included in Suppl. material 3.

Ant identification was carried out following the keys in Fernández et al. (2019), with updates in Camacho et al. (2020) for *Gnamptogenys* s.l. and França et al. (2024) for *Odontomachus*. Three trophic guilds were identified based on

the feeding behaviors and ecological roles of the ants: predators, herbivores (also referred to as phytophages), and omnivores (Brandão et al. 2012).

All specimens were deposited in the "Colección de Artrópodos Terrestres de la Amazonía Colombiana – CATAC" of the Instituto Amazónico de Investigaciones Científicas SINCHI, Leticia, Amazonas. Duplicates of some ant species were deposited in the Colección Nacional de Insectos (CNI), Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia.

## Data analysis

To analyze cohabitation patterns, we constructed a bipartite interaction matrix in which rows represented termite species (lower level) and columns represented ant species (higher level). Each cell contained the number of times a given pair of species co-occurred within the same nesting substrate (i.e., the frequency of cohabitation interactions). Cohabitation occurrence (interaction) was recorded as presence/absence per plot, meaning that the maximum possible cohabitation occurrences per site was eight.

To visualize the interaction networks between termites and ants sharing nests, we used the "plotweb" function from the R package bipartite (Dormann et al. 2008, 2009). From these networks, we extracted modularity (Q), connectance, and nestedness (NODF) using the "networklevel" function as descriptive metrics of interaction density and structural organization. To assess whether observed values of connectance and nestedness were higher than expected by chance, we generated 100 randomized networks using the "r2dtable" null model (Ulrich and Gotelli 2007), which preserves marginal totals, and calculated empirical p-values and z-scores by comparing observed metrics to their null distributions.

To test the significance of modularity (Q), we generated an additional set of 100 randomized networks using the swap algorithm (Gotelli and Entsminger 2003) implemented in the "nullmodel" function and calculated Q values using "computeModules". Observed modularity values were then compared against the null distribution to evaluate deviation from randomness.

Beyond descriptive network-level metrics, we analyzed the topological roles of interacting species by estimating their within-module connectivity (z) and among-module connectivity (c) using the "computeModules" and "czvalues" functions. Based on these values, species were classified as peripherals, connectors, module hubs, or network hubs, following the framework of Olesen et al. (2007). For visual representation of these roles, we constructed z–c plots distinguishing species by their structural positions in the network. All interaction networks were also stratified by forest type and conservation status to assess variation across environmental gradients.

To explore patterns of cohabitation between termite genera and ant trophic guilds (predators, omnivores, and herbivores), we constructed a genus-level interaction matrix based on frequency of co-occurrence. Each termite genus was assigned to a dominant ant guild, defined as the guild with the highest number of associated interactions. We then performed a Principal Component Analysis (PCA) to visualize variation in termite–ant associations using the R packages *vegan* (Oksanen et al. 2019), FactoMineR (Lê et al. 2008), and factoextra (Kassambara and Mundt 2020). To test whether termite genera differed significantly in their interaction profiles based on the dominant ant guild, we conducted a

Permutational Multivariate Analysis of Variance (PERMANOVA) using a Bray–Curtis dissimilarity matrix with 999 permutations (Anderson 2001).

A similar approach was applied to assess the relationship between termite nesting substrates (soil, wood, epigeal, aerial, and soil/wood) and the composition of associated ant genera. For this, we constructed an ant genus-level interaction matrix based on the frequency of co-occurrence in termite nesting substrates. We then conducted a PCA and PERMANOVA, as described above, to evaluate whether termite nesting substrate influenced the assemblage of cohabiting ants.

The Shapiro–Wilk test was conducted to assess the normality of cohabitation occurrences across coverage types, revealing that the data did not follow a normal distribution. Consequently, the Kruskal–Wallis non-parametric one-way analysis of variance was employed to compare cohabitation occurrences among coverage types (Ostertagová et al. 2014). Post hoc pairwise comparisons were performed using "Dunn's test" to evaluate the magnitude and significance of differences among coverages, applying Bonferroni correction for multiple comparisons. The results were visualized using violin plots, generated with the "ggbetweenstats" function from the R package ggstatsplot (Patil 2021).

## Results

A total of 413 specimens were collected across 283 cohabitation networks, with 197 species identified as interacting within these networks. Among these, 110 were ant species, distributed across 36 genera and 10 subfamilies. Additionally, 87 termite species were identified, belonging to 50 genera (five of which could not be identified; see Suppl. material 3), four families, and seven subfamilies within Termitidae.

The termite species with the highest number of cohabiting ant species in their nesting substrates were *Heterotermes tenuis* (11), *Nasutitermes ephratae* (11), *Termes fatalis* (10), *Cylindrotermes parvignathus* (9), *Heterotermes crinitus* (8), Apicotermitinae sp2 (8), and *Araujotermes parvellus* (8). Among ants, the species with the highest number of associations with termite species were *Pseudoponera stigma* (21), *Pheidole* cf. *longiscapa* (10), *Pheidole biconstricta* (9), *Mayaponera arhuaca* (9), and *Camponotus* cf. *orthocephalus* (8). Additionally, *Acropyga tricuspis* and *Ectatomma tuberculatum* were each found cohabiting with seven termite species. In contrast, 31 termite species and 54 ant species were recorded as interacting with only a single species in the cohabitation network.

The cohabitation interactions observed at the species level (Fig. 2A, Suppl. material 2) revealed that only 11.3% (32 interactions) of the total occurred more than once, with *Pseudoponera stigma* being the ant species most frequently involved in these interactions, cohabiting with seven termite species, and *Araujotermes parvellus* being the termite species with the highest number of repeated interactions, cohabiting with three different ant species. Notably, 88.7% (251 interactions) occurred exclusively between a single ant species and a single termite species. These findings indicate a species-level cohabitation network characterized by low generality and a predominance of unique, species-specific interactions, rather than a highly connected structure.

The species-level termite–ant cohabitation network (Fig. 2A) showed moderate connectance (C = 0.279), which did not differ significantly from the null

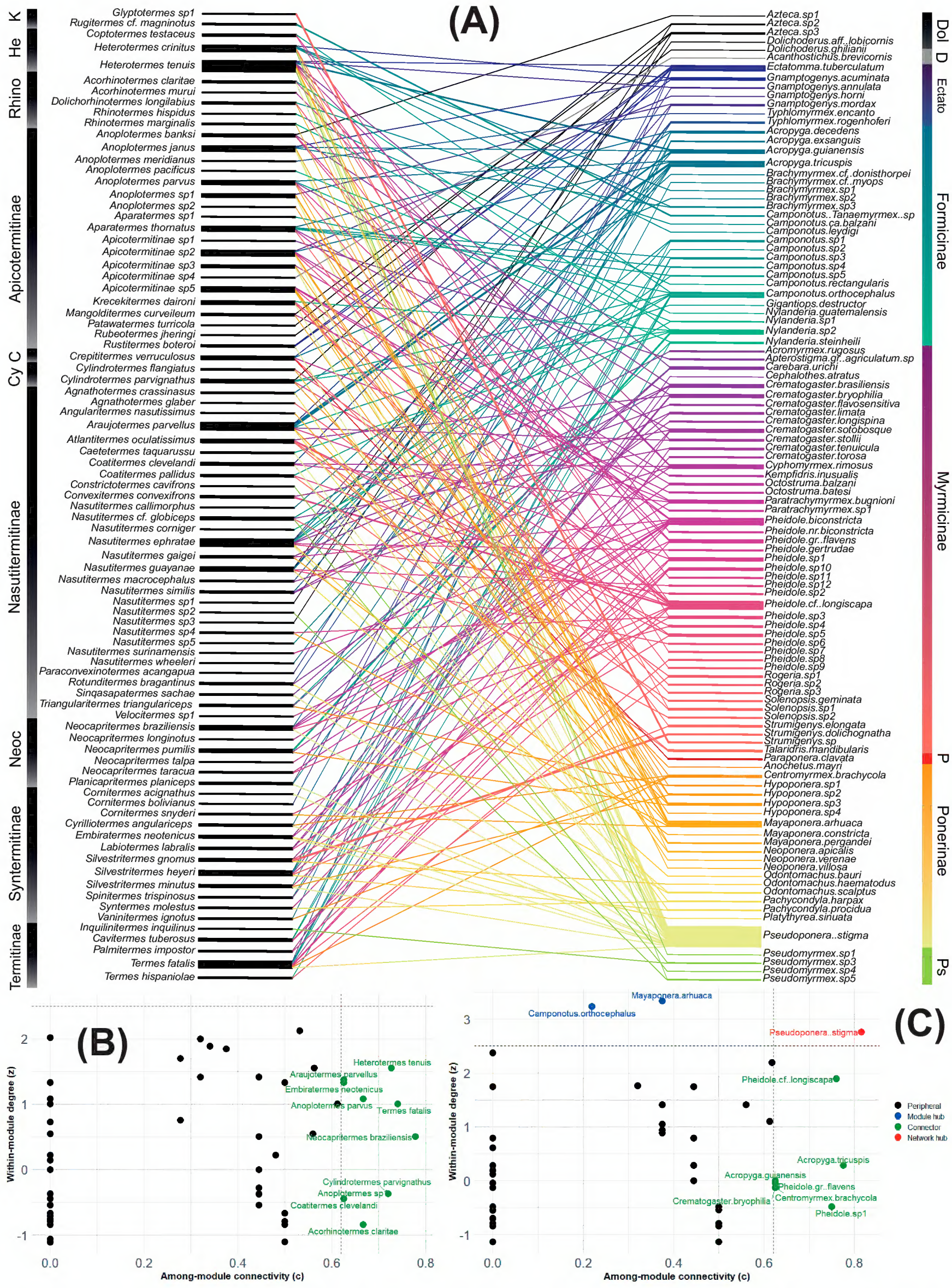


**Figure 2.** Species-level termite–ant cohabitation network and topological roles in Amazonian forests. **A.** Bipartite interaction network showing termite (left) and ant (right) species co-occurring in the same nests. **B, C.** Topological roles of termite species (**B**) and ant species (**C**) based on within-module degree (z) and among-module connectivity (c). Species were classified as peripheral, connectors, module hubs, or network hubs, following the framework of Olesen et al. (2007). Abbreviations: K – Kalotermitidae; He – Heterotermitidae; Rhino – Rhinotermitidae; Cy – Cylindrotermitinae; C – Crepititermitinae; Neoc – Neocapritermitinae; D – Dorylinae; Doli – Dolichoderinae; Ecto – Ectatomminae; F – Formicinae; M – Myrmicinae; P – Paraponerinae; Ps – Pseudomyrmecinae.

model ($p = 0.99$), indicating that the observed proportion of realized interactions could be explained by random processes. However, the network displayed significantly higher modularity than expected under random conditions ($Q = 0.602$, null mean = 0.588, $p < 0.001$, $Z = 1.57$), suggesting that termite–ant associations were structured into distinct modules: clusters of species that interacted more frequently among themselves than with others. In contrast, nestedness was low (NODF = 4.91) and did not differ significantly from null expectations (null mean = 6.30, $p = 0.97$, $Z = -3.29$), indicating that the absence of a nested structure may be compatible with random patterns of cohabitation.

Node-level analysis based on within-module degree (z) and among-module connectivity (c) revealed that the majority of termite and ant species acted as peripherals, interacting mostly within their own modules. Among the 87 termite species analyzed, 10 were classified as connectors, while none reached the thresholds to be considered module or network hubs. In contrast, among the 110 ant species, seven were connectors, two were module hubs, and one species (*Pseudoponera stigma*) acted as a network hub—a central role in bipartite networks.

In termites (Fig. 2B), key connector species included *Neocapritermes braziliensis*, *Termes fatalis*, *Heterotermes tenuis*, and *Araujotermes parvellus*, which exhibited high among-module connectivity ($c \geq 0.62$), suggesting a bridging role among otherwise compartmentalized interaction groups. Despite their structural importance, none of the termite species exhibited z-values above the 2.5 threshold needed to qualify as module hubs.

In ants (Fig. 2C), *Mayaponera arhuaca* and *Camponotus* cf. *orthocephalus* emerged as module hubs, with high z-values ($z > 3$), indicating a central position within their respective modules. *Pseudoponera stigma* stood out as the only network hub, combining high internal and external connectivity ($z = 2.76$; $c = 0.815$). Other structurally relevant ants acting as connectors included species such as *Pheidole* sp1, *Pheidole* cf. *longiscapa*, *Acropyga guianensis*, and *Acropyga tricuspis*.

Primary forests harbored a greater number of connector species compared to secondary forests. In primary forests, most species were peripheral, but eight ant species showed higher connectivity across modules. *Pseudoponera stigma* stood out as a connector ($z > 2$), and *Acropyga tricuspis* was identified as a network hub, exhibiting both high within-module degree and among-module connectivity (Fig. 3B). Other ant species, such as *Camponotus* cf. *orthocephalus*, *Crematogaster brasiliensis*, and *Cretomyrmex brachycola*, also showed relatively high values of among-module connectivity, indicating potential roles in linking different species clusters.

Among termites (Fig. 3C), eight species acted as connectors, showing moderate among-module connectivity, while most termite species remained peripheral. Notably, *Neocapritermes braziliensis*, *Silvestritermes minutus*, and *Heterotermes tenuis* were highlighted as species with the highest c-values in this network.

In contrast, networks in secondary forests were characterized by a predominance of peripheral roles, with no species functioning as network hubs (Fig. 3E, F). In the case of termites, all species were peripheral, indicating limited structural integration across modules in this group. Only two ant species, *Pseudoponera stigma* and *Hypoponera* sp. 3, were classified as connectors, suggesting reduced cross-module interactions.

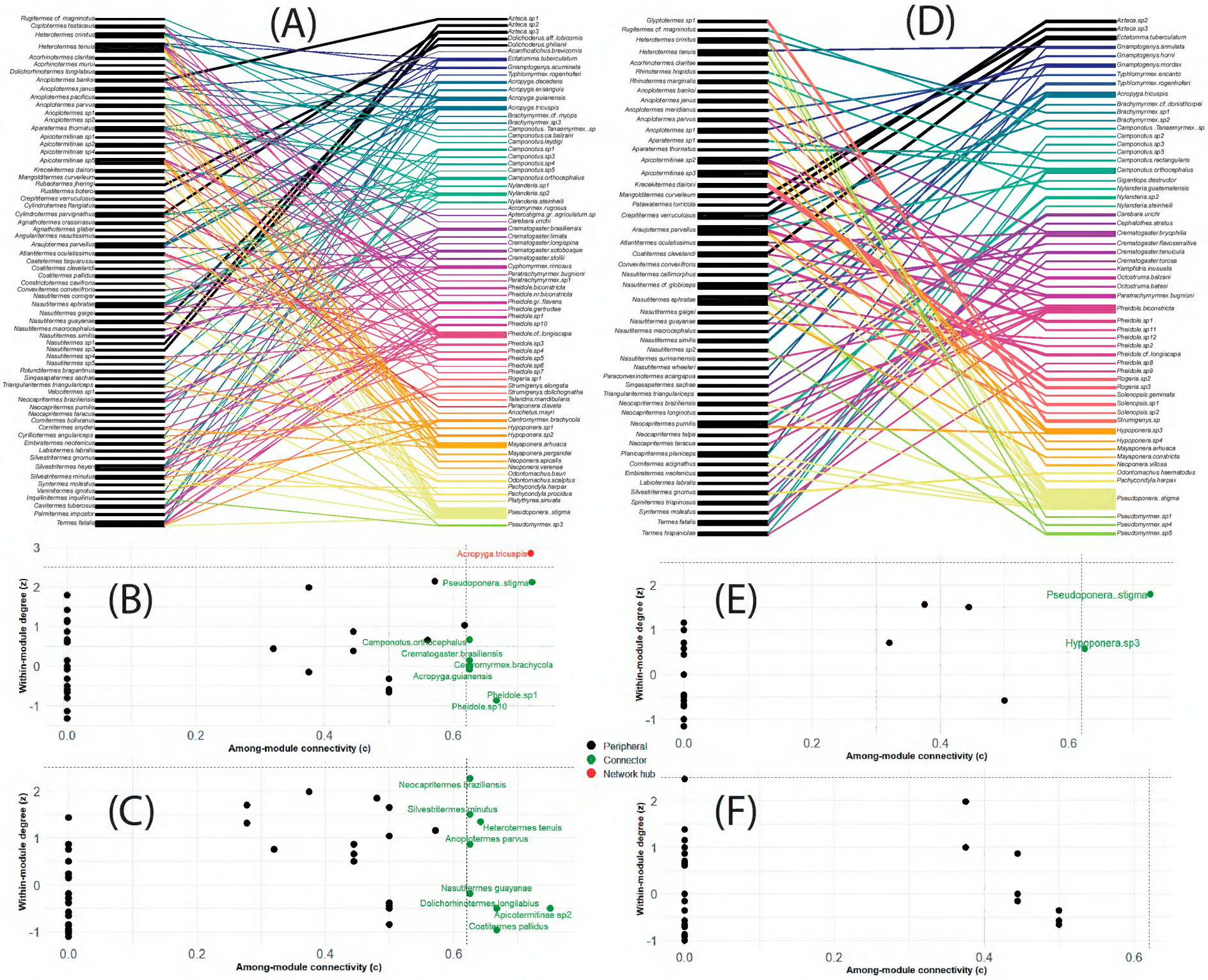


**Figure 3.** Termite–ant cohabitation networks and topological roles across conservation status forests. **A–C.** Primary forests; **D–F.** Secondary forests. Bipartite networks (**A, D**) represent termite–ant cohabitation at the species level. Panels (**B, E**) and (**C, F**) show species roles for ants and termites, respectively, based on within-module degree (z) and among-module connectivity (c). Roles are classified as peripheral, connector, or network hub, following Olesen et al. (2007).

The structure of termite–ant cohabitation networks did not differ significantly between primary and secondary forests in terms of nestedness and connectance, but both showed evidence of non-random modular organization (Fig. 3). In primary forests (Fig. 3A), nestedness (NODF = 4.87) and connectance (C = 0.036) did not differ significantly from null expectations (null means = 6.15 and 0.037, respectively; p = 1 and p = 0.98), indicating no detectable deviation from a random structure in those metrics. However, modularity was significantly higher than expected by chance (Q = 0.66, null mean = 0.62, p < 0.001), suggesting that termite–ant associations were organized into distinct modules more strongly than would occur in a randomized network.

In secondary forests (Fig. 3D), nestedness (NODF = 3.39) and connectance (C = 0.033) were also statistically indistinguishable from the null model (null means = 4.53 and 0.034, respectively; both p = 1). As in primary forests, modularity was significantly higher than expected (Q = 0.79, null mean = 0.76, p < 0.001), revealing a tendency toward non-random compartmentalization.

The termite–ant cohabitation networks differed between terra-firme and seasonally flooded forests in terms of structure and species roles (Fig. 4). In terra-firme

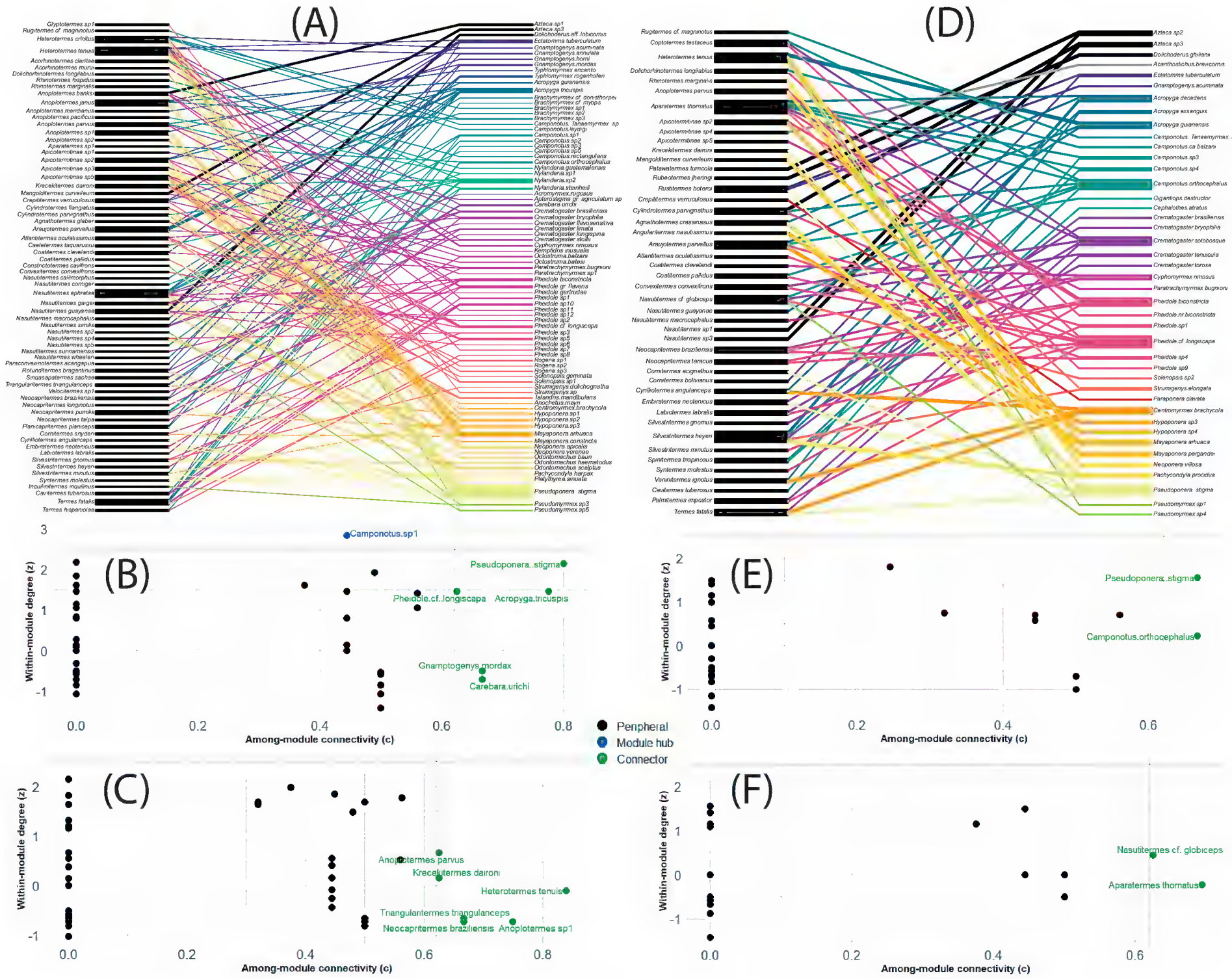


**Figure 4.** Termite–ant cohabitation networks and topological roles across forest types. **A–C.** Terra-firme forests; **D–F.** Seasonally flooded forests. Bipartite networks (**A, D**) represent termite–ant cohabitation at the species level. Panels (**B, E**) and (**C, F**) show species roles for ants and termites, respectively, based on within-module degree (z) and among-module connectivity (c). Roles are classified as peripheral, connector, or network hub, following Olesen et al. (2007).

forests (Fig. 4A), the network showed low nestedness (NODF = 4.46), not significantly different from random expectations (p = 0.99), suggesting that species interactions were not hierarchically organized. Connectance, or the proportion of possible interactions that were realized, was also low and random-like (C = 0.030, p = 0.98). However, modularity was significantly higher than expected by chance (Q = 0.667, p < 0.001), indicating that termite–ant cohabitation in terra-firme forests was non-randomly structured into distinct modules. These patterns suggest structured associations rather than generalized or diffuse interactions.

In seasonally flooded forests (Fig. 4D), the network showed a similar pattern: nestedness (NODF = 4.60, p = 0.91) and connectance (C = 0.046, p = 0.63) did not deviate from null expectations. Modularity was slightly higher than the null expectation (Q = 0.729 vs. null mean = 0.704), but the difference was not statistically significant (p = 0.10), indicating that the apparent modular structure could result from random processes.

Topological role classification based on within-module degree (z) and among-module connectivity (c) showed that most species acted as peripherals in both forest types. In terra-firme forests, *Camponotus* sp1 was identified as

a module hub, exhibiting high within-module connectivity (z) and suggesting a central role within its module. Several ant species acted as connectors, including *Pheidole* cf. *longiscapa*, *Acropyga tricuspis*, and *Gnamptogenys mordax*, while *Pseudoponera stigma* had both high z and c values, suggesting a central role (Fig. 4B). In the termite network, connector roles were found in *Anoplotermes parvus* and *Krecekitermes daironi*, among others with low c-values (Fig. 4C). In flooded forests, *Camponotus* cf. *orthocephalus* and *Pseudoponera stigma* again appeared among the most connected ants, while termites such as *Aparatermes thornatus* and *Nasutitermes* cf. *globiceps* showed moderate among-module connectivity. Therefore, seasonally flooded forest was reported as a less diverse network with fewer connecting species in contrast with terra-firme forest.

Interaction patterns between termite genera and their dominant interacting ant trophic guild differed significantly, as confirmed by PERMANOVA ($F = 12.776$, $R^2 = 0.35$, $p < 0.001$). These differences were largely explained by the first two components of the PCA, which together accounted for 91.8% of the total variation (PC1 = 64.1%, PC2 = 27.7%). While genera associated with omnivorous and predatory ants showed partial overlap in multivariate space, those linked to herbivorous ants were more spatially distinct (Fig. 5).

Out of 50 termite genera, 60% were primarily associated with omnivorous ants, 34% with predatory ants, and only 6% with herbivorous ants. This skewed distribution suggests a stronger ecological coupling between termites and omnivorous or predatory ant guilds. This analysis confirmed that predatory and omnivorous ants exhibited broader associations across termite genera, while herbivorous ants were more restricted.

Genera such as *Acorhinotermes*, *Nasutitermes*, *Aparatermes*, and *Neocapritermes* exhibited broad interaction profiles across guilds, whereas the majority showed more specific affinities. These patterns indicate that the trophic identity of ants may play a structuring role in termite–ant interaction networks, beyond termite taxonomy alone.

Patterns of interaction between ant genera and termite nesting substrates varied significantly, as indicated by PERMANOVA ($F = 6.869$, $R^2 = 0.47$, $p = 0.001$). The principal component analysis (PCA) revealed clear multivariate structuring based on substrate type, with the first two components explaining 73.3% of the variation. While the soil and wood substrates showed broad overlap in multivariate space, aerial and epigeal substrates exhibited more distinct associations (Fig. 6).

The wood substrate supported the highest diversity of ant genera (47%), highlighting its role as a major nesting interface. Ant genera such as *Pheidole*, *Crematogaster*, *Camponotus*, and *Pseudoponera* were associated with multiple substrate types, suggesting generalist nesting behavior. In contrast, soil-associated genera such as *Octostruma*, *Acanthostichus*, *Pachycondyla*, and *Mayaponera* exhibited more specialized nesting preferences. The aerial substrate was closely linked to *Azteca* and other arboreal taxa, while the epigeal substrate showed strong connections with *Odontomachus* and *Strumigenys*. The wood/soil mixed substrate displayed more limited associations, although it maintained interactions with genera like *Paratrachymyrmex* and *Ectatomma*. Notably, the hyperdiverse genus *Pheidole* was recorded across all substrate types, demonstrating the broadest ecological amplitude in nesting associations.

There were significant differences in the number of cohabitation nests across the four forest coverages ($p < 0.05$). Post hoc pairwise comparisons us-

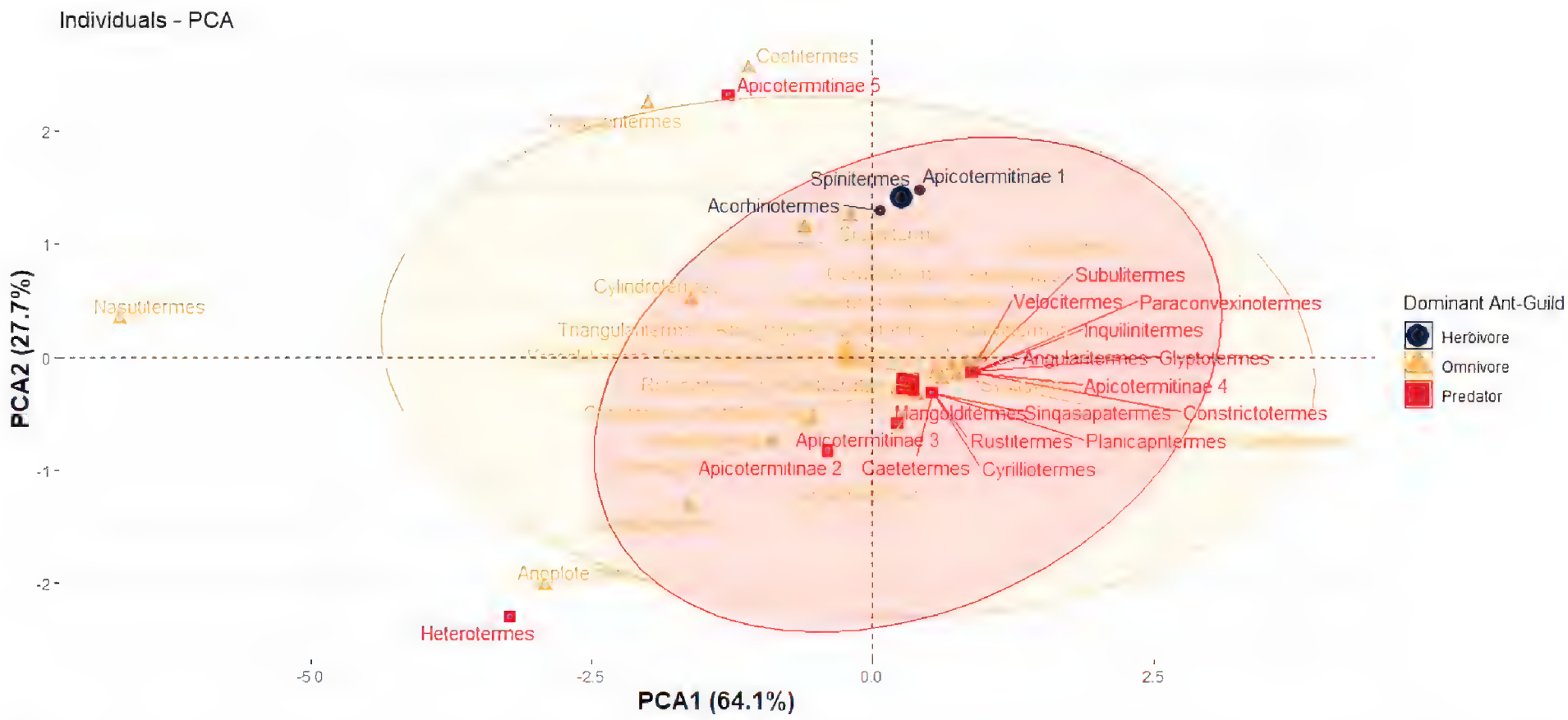


**Figure 5.** Principal component analysis (PCA) of termite genera based on their dominant interacting ant trophic guild. Ellipses indicate 95% confidence intervals. Point size is proportional to the number of interactions recorded for each termite genus.

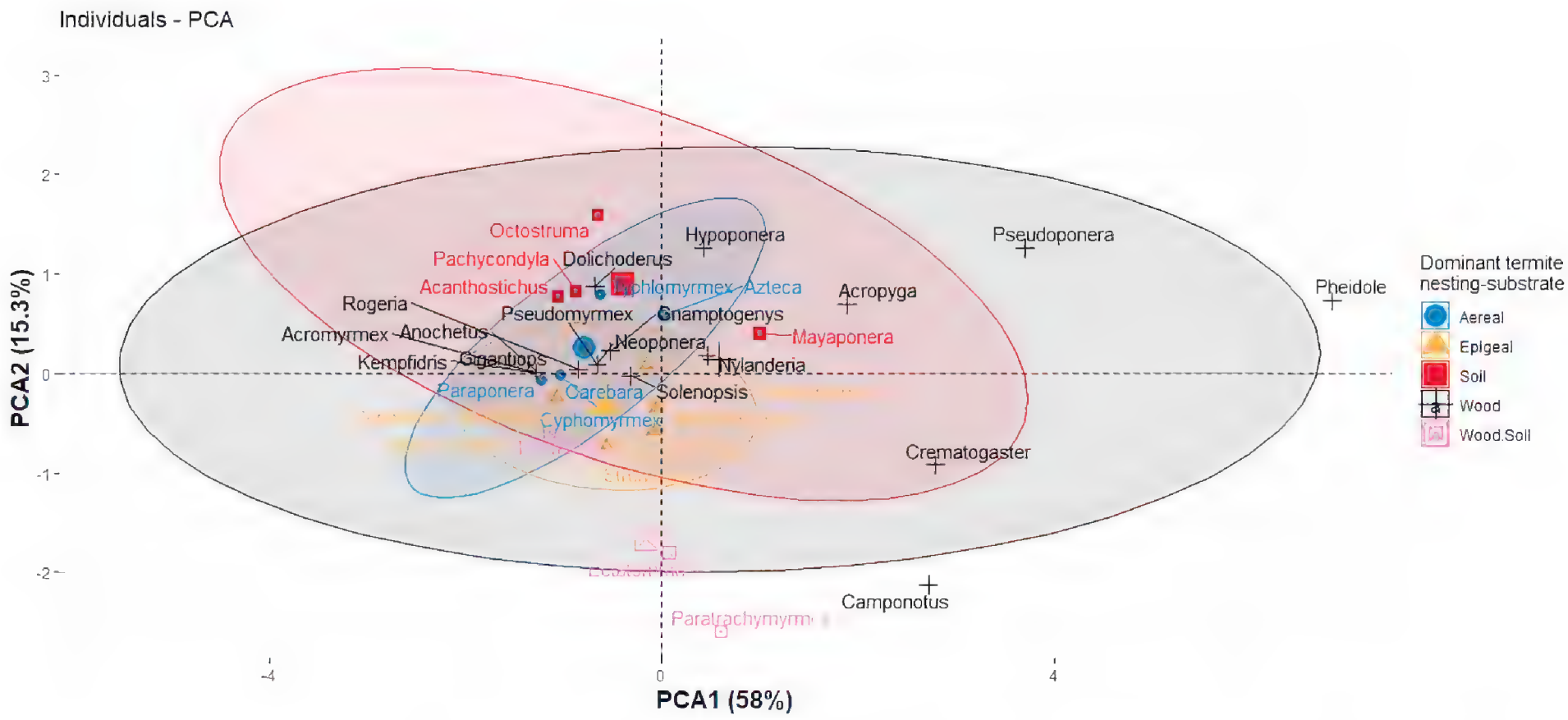


**Figure 6.** Principal component analysis (PCA) of ant genera based on the dominant termite nesting substrate where they were found. Ellipses indicate 95% confidence intervals. Point size is proportional to the number of interactions recorded for each ant genus.

ing Dunn's test, with Bonferroni-adjusted p-values, identified significant differences between seasonally flooded primary forest and both seasonally flooded secondary forest ($p = 0.0096$) and Terra-firme primary forest ($p = 0.006$). The distributions, illustrated by violin plots (Fig. 7), show greater variability in primary forests compared to secondary forests, where cohabitation nests were more restricted. Similarly, the highest number of cohabitation nests was observed in primary forests, reflecting the greater diversity associated with these forest types (Suppl. material 2). These differences highlight the variability in cohabitation nest abundance across forest types, with primary forests exhibiting the highest values and secondary forests the lowest.

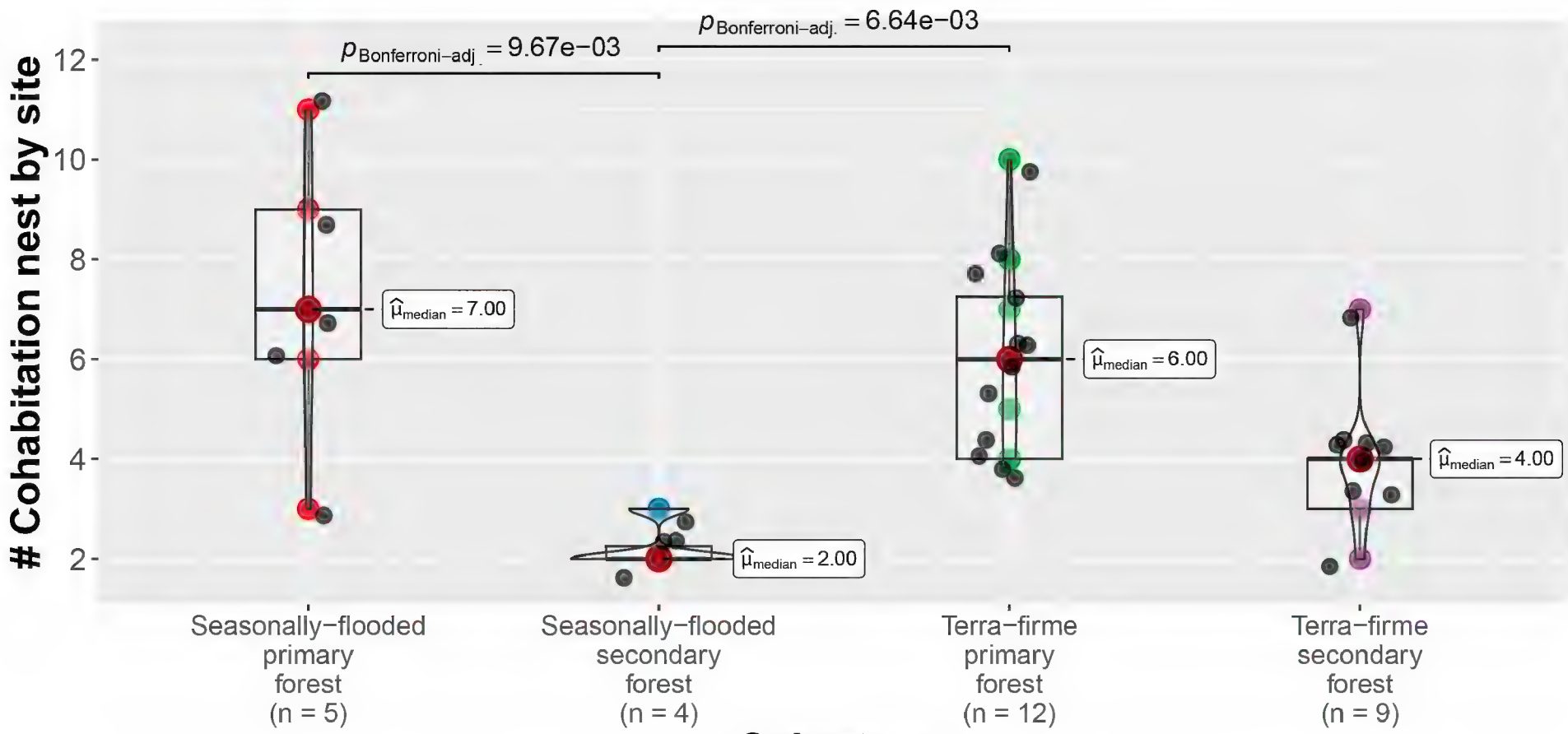


**Figure 7.** Violin plot with boxplots comparing the number of cohabitation nests across four forest coverages using the Kruskal–Wallis test and Dunn's pairwise test. Significant differences (p-values adjusted with Bonferroni correction) are indicated by horizontal bars. Medians are highlighted within each distribution.

## Discussion

The results of this study reveal complex cohabitation networks between ants and termites in Amazonian forests, characterized by low connectance but significantly high modularity. Despite the collection of 110 ant species and 87 termite species, the cohabitation network highlights the taxonomic richness of Amazonian forests. However, only a small fraction of the possible pairwise interactions were observed. This low connectance indicates that most cohabitation events are rare or species-specific, rather than widespread or generalized. However, the significantly higher-than-expected modularity suggests that these interactions are non-randomly structured into discrete modules, where subsets of species interact more frequently among themselves than with others. From a network perspective, the resulting structure reflects a system dominated by weak and scattered associations, with few strong links forming clear interaction clusters.

The collection of termites for diversity studies is primarily constrained by time when using standardized methods (Constantino 2020; Davies et al. 2021), which limits the ability to excavate nests in depth. This limitation may have reduced the likelihood of encountering a greater number of cohabiting ant species, as some termite species have been found to host up to 61 ant species per termite species (Gallego-Ropero et al. 2013). However, the ability to observe a wide variety of nesting substrates, combined with the high species diversity of termites and ants in natural Amazonian ecosystems (Ryder Wilkie et al. 2010; Castro et al. 2018, 2021; Ferreira et al. 2023; Duran-Bautista et al. 2024), revealed the formation of numerous cohabitation interactions.

The emergence of specific interactions aligns with previous findings in Amazonian forests, where generalist interactions in leaf litter had not been reported (Mertl et al. 2012). In contrast, this study documented such interactions in other nesting substrates. The lack of clearly defined modules or highly con-

nected nodes may suggest a more generalized and ecologically diffuse pattern of cohabitation. This observation is consistent with ecological network theory, which proposes that in highly diverse and dynamic ecosystems, such as tropical forests, many interactions can occur at low frequency and may be influenced more by environmental heterogeneity than by strong coevolutionary processes (Vázquez et al. 2009; Poisot et al. 2015; Raimundo et al. 2018).

Modularity was consistently higher than expected under the null model across all forest types, indicating non-random compartmentalization in ant–termite interaction networks. This suggests that species associations are not randomly distributed but instead form distinct modules: groups of interacting species with stronger within-group interactions than between-group connections (Olesen et al. 2007; Dáttilo et al. 2016).

To better understand how individual species contribute to this modular structure, we examined their topological roles within the network. The analysis of within-module connectivity (z) and among-module connectivity (c) revealed the presence of species that act as connectors or hubs, such as *Pseudoponera stigma* and *Camponotus* cf. *orthocephalus*. These species interacted with multiple termite partners across modules, suggesting that they may play key structural roles in linking otherwise disconnected parts of the network. Similar roles have been associated with ecological generalism, behavioral dominance, or flexible nesting habits in other interaction systems (Olesen et al. 2007; Mello et al. 2019).

Although the high proportion of unique interactions in our network could inflate modularity values or limit the detection of strong structural patterns, the ZC framework provides a useful exploratory tool to highlight functionally important species. In understudied systems such as termite–ant cohabitation, where direct functional roles are often unknown, topological descriptors offer valuable proxies for identifying candidate species that may disproportionately shape community structure (Guimerà and Amaral 2005; Campbell et al. 2016). The observed structural positions of certain ant and termite species may therefore reflect variation in nest architecture, species abundance, or degrees of ecological specialization across forest types. We acknowledge that the high proportion of one-to-one interactions in our networks may have inflated modularity estimates due to low interaction frequency or limited detection, as previously noted in sparse ecological networks (Dormann and Strauss 2014). While this analysis is exploratory, it highlights consistent structural patterns that warrant further investigation through expanded sampling.

This interpretation is supported by the finding that modularity was consistently higher than expected across networks. Such pronounced compartmentalization may arise from ecological affinities, microhabitat segregation, or competitive exclusion (Blüthgen et al. 2008). In contrast, lower-than-expected modularity would suggest a diffuse network architecture shaped by generalized resource use or weak interaction specificity (Ulrich and Gotelli 2007; Ulrich et al. 2009). Notably, modular structures are often linked to increased ecological stability, as they can buffer the propagation of disturbances across the network (Stouffer and Bascompte 2011; Grilli et al. 2016).

In our study, modularity likely emerged from structured associations between specific ant functional groups (e.g., generalist predators, dominant species) and particular termite guilds (e.g., soil feeders, wood feeders), as supported by species- and guild-level interaction matrices. These modules may

reflect ecologically meaningful processes such as predation, spatial avoidance, or competition, reinforcing the view that ant–termite co-occurrences are not merely spatial overlaps but the result of ecologically mediated interactions (Tuma et al. 2020).

Although overall connectance was low, the structure of the cohabitation network was influenced by a few termite species that acted as central nodes by interacting with multiple ant species. In particular, species of the genus *Nasutitermes* hosted a large number of organisms due to their ability to build large and aerial nests that provide a fresh and stable refuge (Jaffe et al. 1995; Viana-Junior et al. 2021). This pattern was reflected in our results, as *Nasutitermes* exhibited the highest number of both intraspecific and inter-guild interactions. However, *Heterotermes tenuis* and *H. crinitus*, which do not construct aerial or epigeal nests, also emerged as highly connected nodes. This underscores their ecological role in creating chambers within dry wood that serve as shelters for other species, a function likely driven by their high abundance in Amazonian forests (de Souza and Brown 1994; Junqueira et al. 2009; Duran-Bautista et al. 2020; Castro et al. 2021). The prominence of these termite genera in the network highlights the role of both nest architecture and abundance in shaping the structure of cohabitation.

Wood-based nests yielded the highest number of interactions, surpassing more conspicuous epigeal and arboreal mounds traditionally targeted in cohabitation studies (Costa et al. 2009; Costa and Vanin 2010; Santos et al. 2010; Lisboa et al. 2013; Marins et al. 2016; Schaefer et al. 2016). This underscores the ecological relevance of inconspicuous or cryptic substrates in facilitating multi-species associations. These results suggest that cohabitation is not exclusively associated with the construction of arboreal or epigeal nests but also occurs in other, less-explored substrates, possibly due to lower stability or accessibility.

From a methodological standpoint, our ability to recover the full extent of termite–ant associations was constrained by excavation depth, search time, and the ephemeral nature of some nests. Standardized sampling protocols, while effective for diversity estimates, may underestimate the frequency of rare or transient cohabitation events, especially in substrates like deep soil or highly decayed wood. Moreover, the rarity of many interactions raises challenges for accurately assessing network-level metrics such as nestedness or modularity, which are sensitive to sampling completeness (Blüthgen et al. 2006; Dormann et al. 2009).

Our results suggest that forest type plays a significant role in shaping cohabitation patterns between ants and termites, with primary forests hosting a greater number of shared nesting sites. Specifically, seasonally flooded forests have fewer available nesting substrates compared to terra-firme forests, primarily due to periodic soil flooding (Martius 1994, 1997), which restricts the establishment of termite nests. However, despite this limitation, flooded primary forests exhibited the highest median number of cohabitation events per site (Fig. 7).

This seemingly paradoxical result may be explained by the ecological dynamics described by Pringle et al. (2019), who found that while seasonal flooding negatively affects the diversity and abundance of terrestrial ants, it does not reduce the diversity of arboreal ants. In fact, arboreal ants were more abundant

and exhibited higher biomass in flooded forests than in unflooded ones. These species also showed traits consistent with a greater reliance on plant-derived resources, suggesting behavioral plasticity in response to flooding stress.

Our findings support this interpretation. The cohabiting ant community in our study was dominated by arboreal genera such as *Azteca*, *Crematogaster*, *Camponotus*, and *Pseudomyrmex*. Notably, our network analysis identified *Camponotus* cf. *orthocephalus* as a key connector species in seasonally flooded forest, based on high ZC values, further highlighting the central role of arboreal ants in shaping cohabitation networks. Their dominance, particularly in flooded forests where ground-level nesting is limited, suggests that arboreal ants may increasingly exploit available above-ground termite nests.

However, the most notable difference between forest cover types was associated with forest conservation status. Primary forests, known for their high biodiversity and complex structural diversity (Ackerman et al. 2009; Ryder Wilkie et al. 2010; Mertl et al. 2012; Solar et al. 2016; Dahlsjö et al. 2020), also displayed more intricate cohabitation networks. This finding underscores a direct relationship between cohabitation patterns and ecosystem diversity, highlighting the importance of forest conservation in maintaining these complex ecological interactions.

## Conclusion

This study reveals a diverse but loosely connected cohabitation network between ants and termites in Amazonian forests, characterized by low connectance and high modularity, but without strong compartmentalization by ecological function. Termite species of the genus *Nasutitermes* emerged as key nodes due to their nesting habits, while the high abundance of *Heterotermes* in Amazonian forests facilitated diverse cohabitation. Forest type significantly influenced cohabitation patterns, with primary forests supporting more complex networks than secondary forests, underscoring the importance of forest conservation in maintaining these ecological interactions. Generalist ants, particularly from the genera *Pheidole* and *Camponotus*, contributed to the nested structure of the network by interacting with multiple termite hosts across modules. The predatory species *Pseudoponera stigma* also played a notable role, appearing recurrently across multiple termite nests and modules, suggesting a consistent pattern of co-occurrence that may reflect opportunistic exploitation of termite habitats. Overall, our findings highlight the ecological complexity of ant–termite cohabitation and its strong dependence on habitat diversity and conservation status.

## Acknowledgments

We sincerely thank the indigenous communities for granting us permission to conduct field sampling in their territories. In Amazonas: El Encanto, San Rafael, Santa Rosa, and San Antonio; in Guainía: Ceima Cachivera and Chaquita; in Vaupés: Cerrito Verde and Tucandira. We also extend our gratitude to the civil organizations that allowed us to collect samples on their properties. In Guaviare: Finca La María, Junta de Acción Comunal Damas del Nare, and Asojuntas Charras Boquerón; in Amazonas: Reserva Natural Otra Parte.

We are deeply grateful to Dr. Clara Peña-Venegas for coordinating the soil component at the SINCHI Institute and for her invaluable logistical and administrative support. We also acknowledge Dr. Arleu B. Viana-Junior for his insightful contributions and critical review, which significantly improved this work.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Use of AI

No use of AI was reported.

### Funding

This study was partially funded by the Ministerio de Ciencia, Tecnología e Innovación and the Instituto Amazónico de Investigaciones Científicas SINCHI through the projects "Expedición BIO al sistema lagunar y fluvial del bajo río Guayabero y alto río Guaviare," "Expedición Científica-BIO a la Chorrera (Amazonas), Última Expresión del Escudo Guayanés en Suroccidente de la Amazonia Colombiana," and "Expedición BIO Binacional a la Biodiversidad de la Cuenca del Río Putumayo." Additionally, it was supported by the Colombian government through project BPIN 202300000000285, "Investigación científica transformativa para potenciar el bienestar, la conservación y la gobernanza ambiental en la Amazonia colombiana" (Amazonas, Caquetá, Guainía, Guaviare, Meta, Putumayo, Vaupés).

### Author contributions

Conceptualization, D.C. and F.F.; methodology, D.C. and F.F.; software, D.C.; validation, D.C.; formal analysis, D.C.; investigation, D.C. and F.F.; resources, D.C.; data curation, D.C.; writing—original draft preparation, D.C.; writing—review and editing, D.C. and F.F.; visualization, D.C. All authors read and approved the final version of the manuscript.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Description of sampled sites in this study

Authors: Daniel Castro, Fernando Fernández

Data type: docx

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Link: https://doi.org/10.3897/neotropical.20.e154485.suppl1

## Supplementary material 2

### List of termite species and their cohabiting ant species found in termite nests in Amazonian forests

Authors: Daniel Castro, Fernando Fernández

Data type: docx

Explanation note: Nest types: A: aereal nest; E: epigeal nest; S: soil; W: wood; W/S: highly decomposed wood.

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Link: https://doi.org/10.3897/neotropical.20.e154485.suppl2

## Supplementary material 3

### Enteric valves of termite morphospecies from the Apicotermitinae subfamily

Authors: Daniel Castro, Fernando Fernández

Data type: docx

Explanation note: (A) Apicotermitinae 1, (B) Apicotermitinae 2, (C) Apicotermitinae 3, (D) Apicotermitinae 4, (E) Apicotermitinae 5.

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